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THE MUTATIONS OF OENOTHERA STENOMERES

H. H. Bartlett

This preliminary article on the mutations of *Oenothera stenomeres* Bartlett is presented now in order to substantiate certain statements in a paper contributed by the writer to the symposium on the genetic relationships of organisms, held at the recent Philadelphia meeting of the Botanical Society of America. The papers of the symposium will appear in this Journal next month. Some of the mutations of *Oe. pratincola* Bartlett, which were also referred to, are dealt with in an article which have been published elsewhere.[1] A brief statement in regard to the mutability of *Oe. stenomeres* may be found in an earlier number of this journal[2] to which reference must be made for a full characterization of the species. The two mutations are mut. *lasiopetala* and mut. *gigas;* the former has occurred five times in the cultures of the first four generations, the latter but once. These cultures may be summarized as follows:

P			Unknown.
F_1	1910		A single plant, culture No. 32, transplanted into the garden from the wild and self-pollinated; f. *typica*.
F_2	1911	∞	Progeny of No. 32, 10 plants; f. *typica*.
F_3	1912	∞	Progeny of No. 32–4, 8 plants; f. *typica*.
F_3	1914		Progeny of No. 32–4, 4 plants; 3 mut. *lasiopetala*, 1 f. *typica*.
F_3	1912	∞	Progeny of No. 32–6, 8 plants; f. *typica*.
F_3	1914		Progeny of No. 32–6, 80 plants; f. *typica*.
F_3	1914		Progeny of No. 32–9, 7 plants; 1 dwarf, 6 f. *typica*.
F_4	1913		Progeny of No. 32–4–6, 106 plants; 1 self-sterile, 1 mut. *lasiopetala*, 1 mut. *gigas*, 103 f. *typica*.
F_4	1914		Progeny of No. 32–4–6, 96 plants; 1 mut. *lasiopetala*, 95 f. *typica*.

The object of growing the cultures of 1910, 1911 and 1912 was primarily systematic, and the garden space was small. Consequently only a few plants were brought to maturity. In the summary above I have indicated by the sign ∞ the cultures in which germination was normal and from which most of the seedlings were discarded. In the other cultures germination was poor, and all the plants were kept. It will be noticed that mutations were found only in the cultures characterized by poor germination. The writer usually sows the seeds from two or three capsules (400–900 seeds) in each germination pan. Unfortunately, the seeds were not counted for any sowings of *Oe. stenomeres*. In 1913, the first year in which plenty of garden space was available, all of the seedlings obtained were kept until maturity, and in that year the two mutations, mut. *lasiopetala* and mut. *gigas*, were discovered. In the following year several packets of old seeds, which has been left over from previous plantings, were sown, with the result that one lot of possibly a thousand old seeds gave only four plants, of which 3 were mut. *lasiopetala* and one was forma *typica*. The same seeds, two years before, had germinated normally and the young seedlings appeared uniform. Eight of them, carried to maturity, were all f. *typica*. It is clear that mut. *lasiopetala* is a mutation of infrequent occurrence, but that the seeds which give rise to it are for some reason longer-lived than those of f. *typica*. The phenomenon of selective mortality is probably very important in the operation of natural selection. In the article on *Oe. pratincola* mut. *nummularia* (l. c.) very clear evidence of differential fermination and selective mortality is presented. In the case of *Oe. stenomeres* mut. *lasiopetala* the latter phenomenon seems to account for the unexpected composition of small cultures.

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[1] Bartlett, H. H. Additional Evidence of Mutation in Oenothera. Bot. Gaz. **59**: 81–123. 1915.

[2] Bartlett, H. H. An Account of the Cruciate-flowered Oenotheras of the Subgenus Onagra. Amer. Journ. Bot. 1: 226–243. 1914.

Oe. stenomeres mut. **lasiopetala** nom. nov.[3]

Before the rosettes of this mutation have attained a diameter of 2 cm. they may be distinguished from the type form by their more densely pubescent, broader, sometimes almost orbicular leaves. The leaves of f. *typica* are ovate. Differences become more pronounced as the plants grow older. The mutation remains persistently in the rosette condition. The rosettes of the type, on the contrary, are transitory, for the species is an annual. The mature foliage of the mutation is so densely pubescent that it looks gray in comparison with the green foliage of the type.

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[3] The name of this mutation was originally published as *Oe. stenopetala* mut. *lasiopetala* (Amer. Journ. Bot. 1: 237. 1914). The specific name *Oe. stenopetala* had been used in the writer's paper as originally submitted for publication, but was later altered to *Oe. stenomeres* on account of the prior publication of *Oe. stenopetala* Bicknell. In one place the preempted name escaped correction in the proof. The oversight is especially regretted because Mr. Bicknell's new species is likewise one of the cruciate Onagrae. It is not, however, at all closely allied to *Oe. stenomeres*, not has it yet been made the subject of experimental study.

Among the five primary mutations and 44 F_1 plants of mut. *lasiopetala* which have been under observation only one plant has so far flowered. All of the few plants which became cauline formed rosettes at the ends of the stem and branches instead of flowering. Only in the case of the plant shown in figure 1, a single branch flowered late in the fall of 1913 and produced three capsules of seeds. All of the other branches, and the main stem, bore rosettes in every way like the radical rosette. In 1914 no seeds were obtained. The most striking feature of mut. *lasiopetala*, the hairiness of the petals, has therefore been observed in only one plant. The pollen was examined and was found to have three germination points, as in the parent form. Perhaps one grain in a hundred was found to have four points, as in mut. *gigas*. In f. *typica* 60 to 80 per cent of the pollen grains are perfect; in mut.

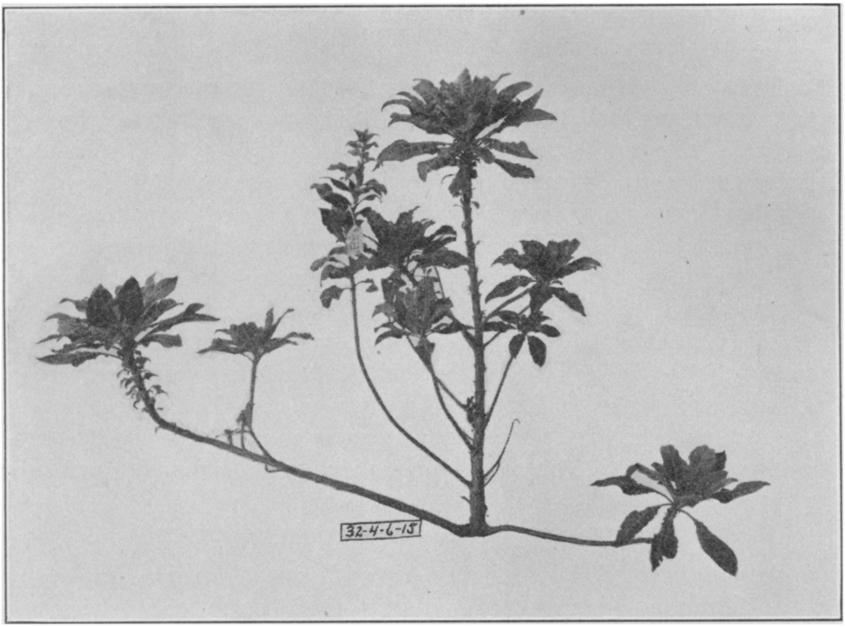

FIG. 1. The original plant of *Oe. stenomeres* mut. *lasiopetala*, no. 32–4–6–15. The label on the ground is 10 cm. long.

lasiopetala between 40 and 50 per cent are perfect, the remainder shrivelled and defective.

The F_1 progeny of mut. *lasiopetala*, from self-pollinated seeds of no. 32–4–6–15, may be summarized as follows:

	Seeds	Plants	F. *typica*	Mut. *lasiopetala*	Other muts.
Capsule *A*	78	26	—	—	—
Capsule *B*	122	39	—	—	—
Capsule *C*	156	51	—	—	—
Total F_1	356	116	70	44	2

The progeny consisted of 60 per cent. f. *typica* and 40 per cent. mut. *lasiopetala*. The two types were distinguished at a very early age. The mode of inheritance is comparable to that of two of the mutations from *Oe. Lamarckiana* Hort. namely *Oe. lata* de Vries and *Oe. scintillans* de Vries. The former is generally self-sterile for the reason that it produces no good pollen: de Vries,[4] however, succeeded in deriving a fertile strain from the cross *Oe. lata*×*semilata*, and found that its progeny by self-pollination consisted of *Oe. lata* and *Oe. Lamarckiana*, just as would have been the case if the pollen had been derived from *Oe. Lamarckiana*. In other words, it appears that the good pollen grains of *Oe. lata* are genetically the same as those of *Oe. Lamarckiana*, and do not carry the *lata*-characters. This conclusion is borne out by the fact that *lata*-like fertile hybrids between *Oe. lata* de Vries and *Oe. Hookeri* T. & G. cannot transmit the *lata*-characters through the pollen, and transmit to only a portion of their progeny through the eggs. *Oe. scintillans* acts like *Oe. lata* in every way; its pollen, moreover, is always sufficient for self-pollination.

Thus it appears that there is a class of mutations of which the eggs are of two kinds; one kind carries the characters of the parent species, the other kind the characters of the mutation. The pollen grains, however, appear to be of one kind only, and to carry the characters of the parent species. Is it not possible that the male gametes which carry the characters of the mutation are eliminated because of some physiological defect? If so, *Oe. lata* might be supposed to originate by the union of a *lata*-egg (itself constituting the true mutation) with a *Lamarckiana*-sperm. Then *Oe. lata* would be a heterozygote, and would produce gametes of two kinds. If the male *lata*-gametes were eliminated, the progeny of *Oe. lata* would consist of both *Oe. lata* and

[4] Gruppenweise Artbildung, p. 256.

Oe. Lamarckiana, quite regardless of whether the pollen was derived from the heterozygous mutation or the homozygous parent species. A partial elimination of *lata*-eggs would explain the deviation from the expected 1 : 1 ratio, for the mutational form rarely constitutes a full half of the progeny. The pollen of *Oe. lata* is so much more highly defective than the ovules that this hypothesis seems not an improbable one. Gates and Thomas[5] have shown that in *Oe. lata* the cytological facts are in accord with such an explanation. The somatic number of chromosomes is 15, whereas in *Oe. Lamarckiana* it is but 14. *Oe. lata* therefore produces two classes of gametes, with 8 and 7 chromosomes, respectively. If two 7-gametes fuse, we have *Oe. Lamarckiana;* if a 7-gamete (presumably male) fuses with an 8-gamete (presumably always female) we have *Oe. lata.* Plants with 16 chromosomes have not been found. From this fact, and the data in regard to inheritance, we must assume that the male 8-gametes are eliminated.

There is clearly no reason why mutations which follow the *lata*-type of inheritance should not be viewed as progressive in their nature, even though they exist only as heterozygotes. Thus far only three such are known, *Oe. lata*, *Oe. scintillans* and the new *Oe. stenomeres* mut. *lasiopetala*.

Oe. stenomeres mut. **gigas,** mut. nov.

This rare mutation was found in the same progeny which included the first example of mut. *lasiopetala*. So far only one specimen has appeared. In the former paper (l. c., p. 236) it was merely referred to as a mutation with "very large, thick buds and short, thick fruits." It was even then thought to be a *gigas*-mutation, but was not named because a chromosome count had not yet been made. Mr. E. G. Arzberger has now found the chromosome number to be 28. Cytologically and morphologically there is perfect analogy between *Oe. stenomeres* mut. *gigas* Bartlett and *Oe. gigas* de Vries. Each is more persistently biennial than its parent form and has thicker, broader leaves, stouter stems, larger buds, thicker fruits, 4-pointed instead of 3-pointed pollen, and twice as many chromosomes. Each is characterized by a strongly rosuliferous rather than freely branched main stem, and bears its branches mainly in the axils of the rosette leaves. Each is marked by a greater range of variation than its parent form, in that it gives rise

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[5] Gates, R. R. and Thomas, Nesta. A Cytological Study of *Oenothera* mut. *lata* and *Oe.* mut. *semilata* in Relation to Mutation. Quart Journ. Micr. Sci. **59**: 523–571. 1914.

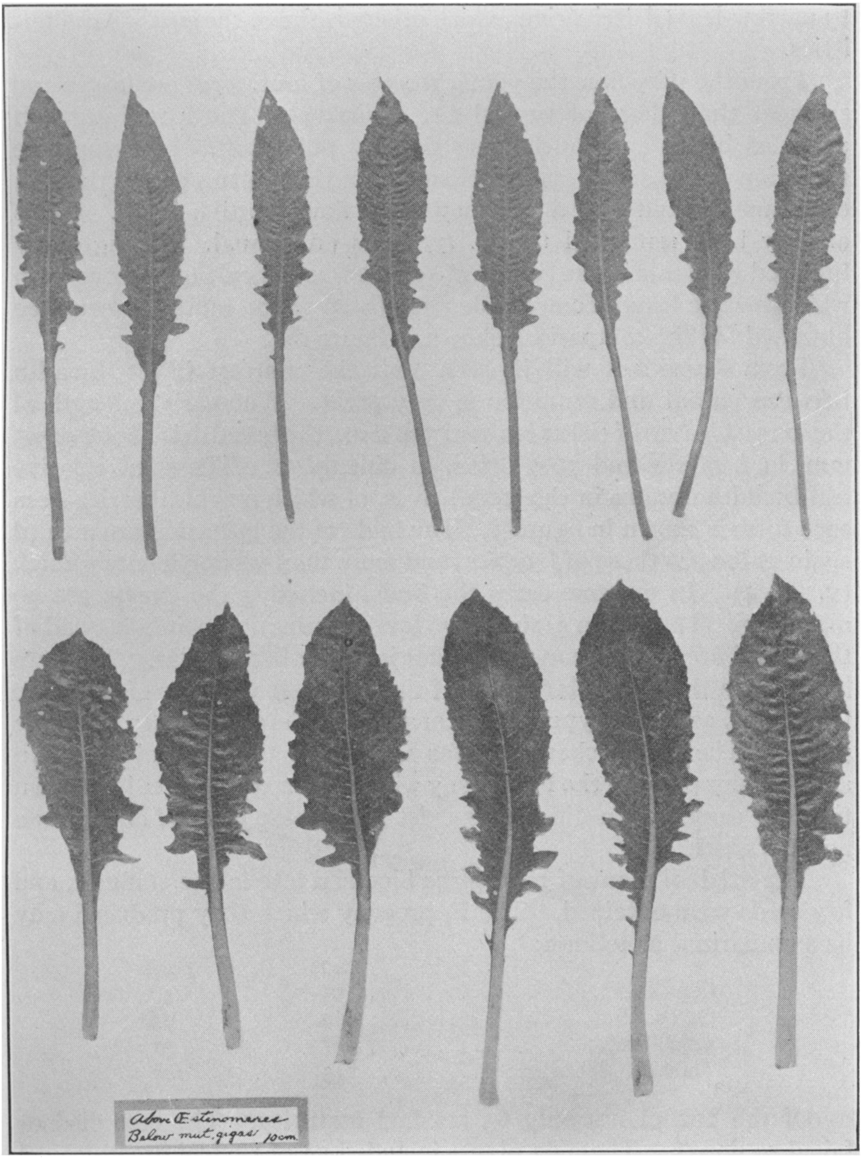

FIG. 2. Rosette leaves of *Oe. stenomeres* f. *typica* (above) and mut., *gigas* (below). The label is 10 cm. long.

to narrow-leaved derivatives which otherwise have the *gigas*-characteristics.

From the very first the young rosettes of mut. *gigas* are larger and stronger than those of typical *Oe. stenomeres*. The leaves are half again as broad and much more densely pubescent. In nature the mutation would doubtless be a biennial, for the rosettes persist through early summer and have a tendency not to flower until late fall. It has already been remarked that f. *typica* is an annual. Among many hundred F_5 plants in the garden of 1914 it was difficult to find one from which rosette leaves comparable with those of the mutation could be obtained for the comparison shown in figure 2.

From figure 2 it will be seen that the contrast in leaf-breadth between parent and mutation is very great. Whereas the length of the longest leaves of either is about 300 mm., the breadth is about 40–45 mm. in f. *typica* and 70–75 mm. in mut. *gigas*. The same relative leaf-breadth obtains in the stem leaves, of which a typical series from each form is shown in figure 3. The buds of the mutation are a third again as long as those of f. *typica*, and more than proportionately thick (v. fig. 4). In extreme cases the buds, including the ovary, are 90 mm. long. The pollen grains have four germination points instead of three, and are therefore quadrangular instead of triangular. They are larger than the triangular grains of the type. A very few of them are triangular, as in the type, and a considerably larger number have five points. The pollen character was verified in the original mutation and in every plant of the F_1 progeny which bloomed. Gates has shown that the same pollen differences exist in the case of *Oe. Lamarckiana* and *Oe. gigas*.

The original plant of mut. *gigas* bloomed late in the summer, and few seeds were obtained. The F_1 progeny which they produced may be summarized as follows:

	Seeds	Plants
Capsule *A*	91	46
Capsule *B*	69	25
3 small capsules	85	31
Total F_1	245	102

Of the 102 plants only 63 reached maturity. The rest died or failed to flower. These 63 plants included 54 of typical broad-leaved mut. *gigas*, 6 narrow-leaved variations otherwise similar to mut. *gigas*, and 3 secondary mutations. Of the secondary mutations two were

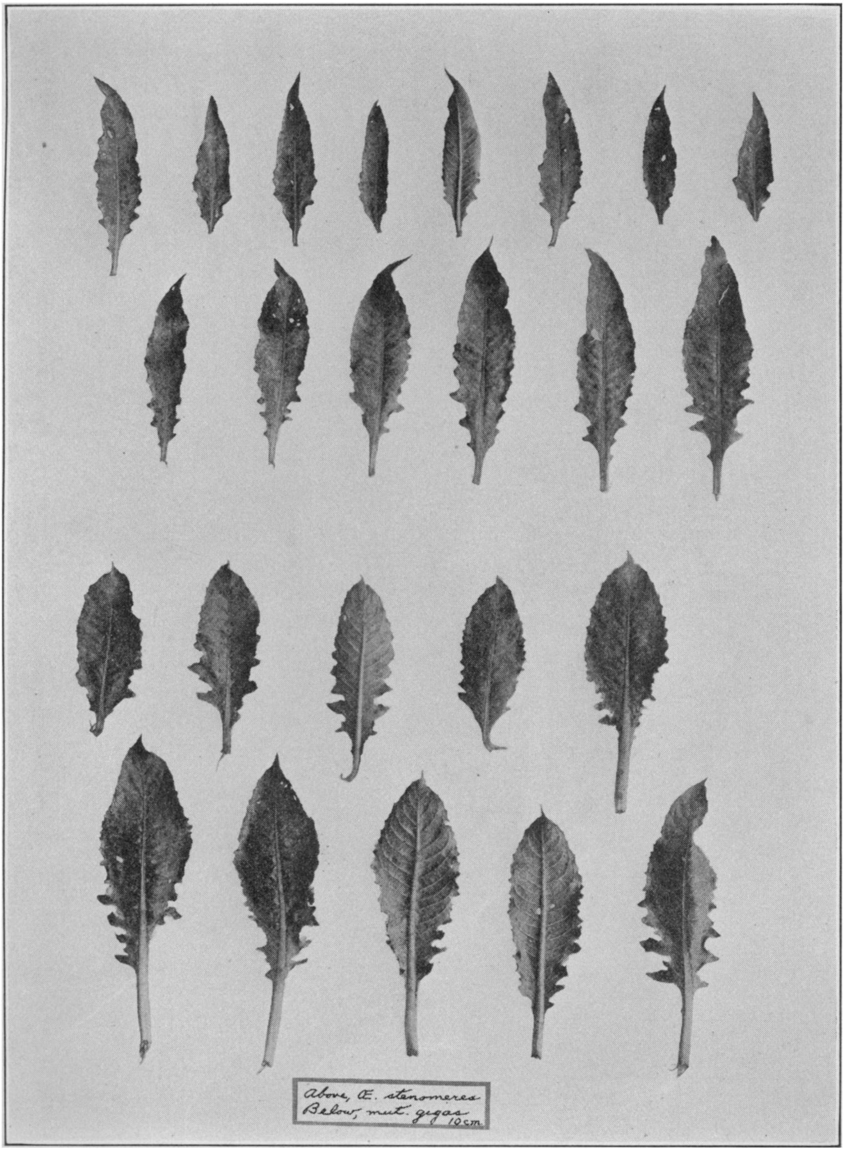

Fig. 3. Stem leaves of *Oe. stenomeres* f. *typica* (above) and mut. *gigas* (below). The label is 10 cm. long.

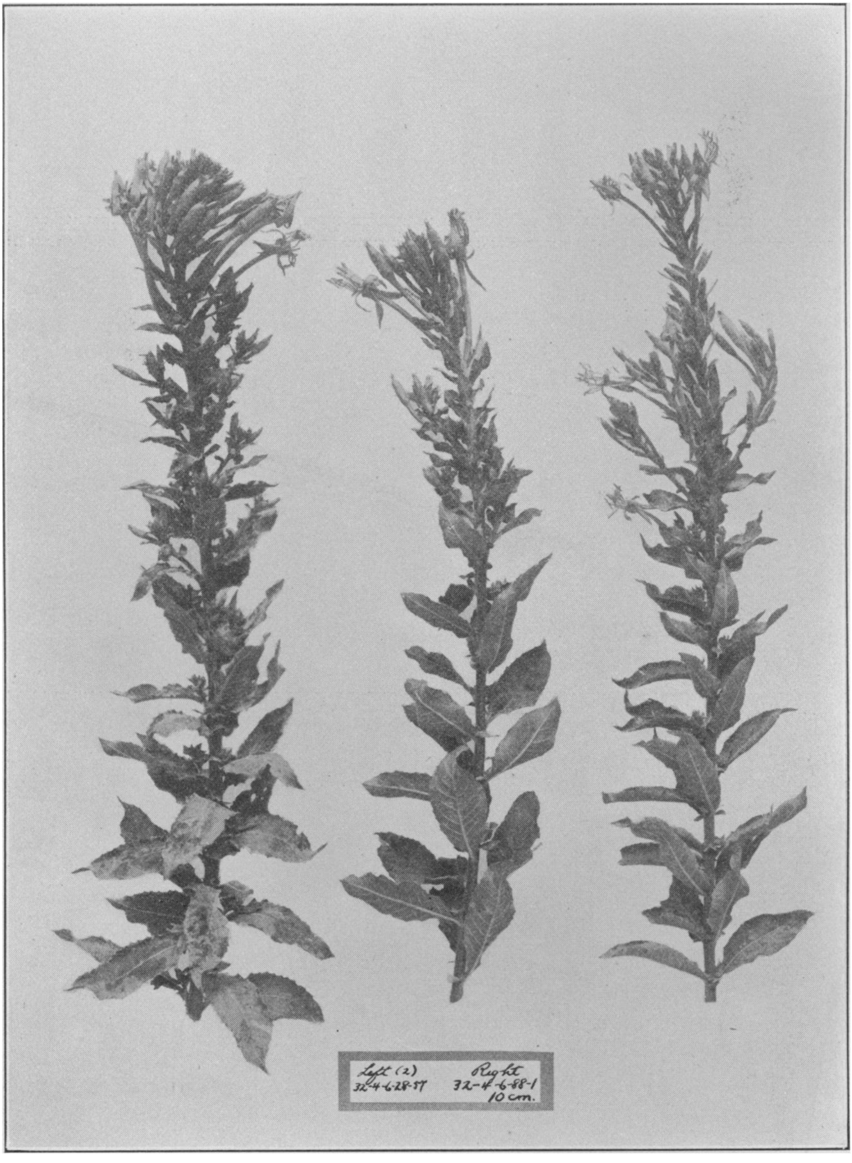

FIG. 4. Inflorescences of main stem of *Oe. stenomeres* f. *typica* (right) and mut. *gigas* (left). Inflorescence of basal branch of mut. *gigas* (center). The label is 10 cm. long.

dwarfs, and one corresponded to mut. *lasiopetala* from f. *typica*. It may be called *Oe. stenomeres* mut. *gigas*$_1$ *lanosa*$_2$. Not only were the petals hairy, as in mut. *lasiopetala*, but the filaments of the stamens alternate with the petals were densely lanose. The filaments of the other four stamens were glabrous. This plant was just coming into flower at the time of the first killing frost. It had to be removed to the greenhouse and does not give much promise of yielding seeds.

The plants which failed to flower appeared to have the *gigas*-characteristics. It will be remembered that *Oe. gigas* de Vries also bred true from the first appearance of the mutation.

Conclusion

The point which should be especially emphasized in connection with the mutations of *Oe. stenomeres* is that neither of them can be interpreted as the result of segregation following hybridization. *Oe. stenomeres* is an isolated cruciate species, related to none of the other cruciate species, and geographically remote from all of them. The peculiarities which characterize mut. *lasiopetala* are not known in any other species and cannot, therefore, be construed as having been introduced into *Oe. stenomeres* by hybridization with any other type. It seems more likely that *Oe. stenomeres* itself originated by mutation from some broad-petaled elementary species allied to *Oe. gauroides* Hornem., and that mut. *lasiopetala* constitutes a second mutation in the same direction. The occurrence of mut. *gigas* cannot be viewed as even remotely due to hybridization, for the characters of this mutation can be explained on a cytological basis.

Like most of the other *Onagrae*, *Oe. stenomeres* shows a considerable degree of pollen sterility. This sterility we may view as a sign of the prevalence of mutation in the group. Both mutation and hybridization bring about pollen sterility, and both processes are widely prevalent in the subgenus Onagra. It is illogical and unjustifiable to state, as certain authors have done, that the mutability is the result of the hybridity. It seems far more probable that the truth is exactly the opposite. Far from having proved that hybridization "explains" mutation, no one has yet even shown how hybridization *could* explain it. Finally, attention may again be called to the fact that *Oe. stenomeres* is a close-pollinated and practically a cleistogamous species in nature, and that its mutability was not discovered until the fourth generation of a guarded line was grown.

BUREAU OF PLANT INDUSTRY, WASHINGTON